

Are *Eulemur* Species Pair-Bonded? Social Organization and Mating Strategies in *Eulemur fulvus rufus* From 1988–1995 in Southeast Madagascar

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ABSTRACT Strong social relationships have been reported between adult male and female prosimian primates in the genera *Eulemur* and *Varecia* and have been referred to as “pair-bonding.” It has been hypothesized that females benefit from these affiliative relationships with an adult male by having protection against infanticidal males, implying that the male member of the dyad also is the father of her offspring. I evaluated this hypothesis and whether or not the term pair-bond was appropriate by using field data collected on two groups of *Eulemur fulvus rufus* in southeastern Madagascar. Four predictions were tested: 1) male–female dyads will be stable throughout the year, 2) male–female dyads will be more prevalent during the mating season, and/or the birth season when infants would be most vulnerable to infanticide, 3) females should copulate either exclusively or most often with their male dyad partner than with other males during the mating and/or birth season, and 4) rates of aggression will be higher between males or between females and males who are not their dyad partner. Predictions 1, 2, and 3 were not supported and Prediction 4 was only partially supported. Adult male–female dyads however, were more prominent in feeding contexts during the mating season and food scarcity periods. Most aggression occurred during feeding between males and nondyad group members. Since female feeding rates were often higher when feeding near male dyad partners, adult male–female dyads may serve as a way of increasing foraging efficiency for the female, which in turn may influence reproductive success. All males who were dyad partners also copulated first and more frequently with all females. It is suggested that “dyad” is a better descriptive term than pair-bonding for the social patterns observed since dyads were comprised of same-sex individuals, were temporary, and did not exclusively serve a reproductive function. *Am J Phys Anthropol* 105:153–166, 1998. © 1998 Wiley-Liss, Inc.

Pair-bonding and monogamy are two terms that are often used interchangeably when describing primate social systems. As Kinzey (1987) noted, however, these two terms are distinct. Monogamy refers to an exclusive reproductive relationship between a male and female (Wickler and Seibt, 1983) while pair-bonding refers to a permanent social relationship between two individuals that may not necessarily include exclusive

mating privileges (Eisenberg et al., 1972). By these definitions, most monogamous pri-

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mates are also pair-bonded, but it is possible that primates could be pair-bonded socially and not maintain a monogamous mating system. Many studies have been conducted on the behavioral and ecological correlates to monogamy in nonhuman primates (Tilson and Tenaza, 1976; Kleiman, 1977; Pollock, 1977; Brockelman and Shrikosamatara, 1984; Mitani, 1984; Wright, 1984, 1985; Mendoza and Mason, 1986; Leighton, 1987; Mock and Fujioka, 1990; van Schaik and Dunbar, 1990; Palombit, 1995), but unfortunately we know little about pair-bonding in larger groups. Many researchers have noted that adult males and females form affiliative relationships outside the mating season and have identified them as "friendships" or as strong affiliations between dyads rather than labeling them as pair-bonds (Smuts, 1985; Manson, 1994; Rose, 1994; Gould, 1996a).

Van Schaik and Kappeler (1993), however, recently summarized reports of consistent male-female dyads (which they referred to as pair-bonds) in the prosimian genera *Eulemur* and *Varecia*, which live in groups containing multiple adult males and females. They hypothesized that dyads form in these species so that males can protect a female and their infant from infanticidal attempts by other males (see also van Schaik and Dunbar, 1990, for gibbons). An exclusive reproductive relationship between the two members of the dyad is implied by their argument since males are presumably protecting their reproductive investment by guarding their infants. This hypothesis (referred to as the Infanticide Prevention Hypothesis) and whether or not the term pair-bond is appropriate for lemurid species has yet to be tested using field data. In addition, alternative explanations have not been considered for this type of social organization in lemurid primates.

If adult male and female dyads are formed as a way for males to protect their reproductive investment (essentially a type of mate defense), four predictions can be generated from the infanticide prevention hypothesis and tested. First, adult male-female dyads should be stable throughout the year to be considered a pair-bond. Second, even if adult male-female dyads are not stable throughout the year, they should be more prevalent

during the mating and birth seasons if they are to serve an exclusive reproductive function. Each male should maintain close spatial proximity to a female during the mating season to ensure that she mates exclusively with him. If males function as infant-protectors, they should also be in closer spatial proximity to females when infants are more vulnerable to infanticide, especially during early lactation. Direct observations of males defending infants against other males would also lend support for the infant prevention hypothesis. Third, a female should copulate either exclusively or more often with her preferred male partner than with other males. A male presumably would be less likely to defend an infant against attack unless they were assured of paternity. Fourth, rates of aggression should be higher between nondyad group members than within the dyad. Rates of aggression also will be highest between males during a) the mating season if males are trying to maintain exclusive reproductive access to females, and b) the birth season if males are targeting potentially infanticidal males. In addition, females are expected to target other males (other than their dyad partners) during the birth season to protect their infants.

The infanticide prevention hypothesis is similar to other hypotheses offered to explain nonsexual affiliations between males and females in some anthropoids such as baboons (Smuts, 1985) or macaques (Manson, 1994). In these examples, males protect females from aggression from other group members, but not infanticidal males specifically. Some of the other "services" provided by males in the context of male-female affiliative relationships in anthropoids also may help explain why male-female dyads are common in lemurs (see Jolly, in press). These include: increased infant care (Wright, 1984; Smuts, 1985), increased predator detection (Dunbar, 1988), or increased foraging success, which in turn can increase reproductive success (Hill, 1990). Another possibility is that lemurs may increase thermoregulation through huddling behavior (Morland, 1993), although the sex of the social partner is not a crucial element to this hypothesis.

The predictions derived from the infanticide prevention hypothesis was tested in this study using data collected on two wild groups of rufous lemurs (or red-fronted lemurs, *Eulemur fulvus rufus*) at the Ranomafana National Park in southeast Madagascar. Both rufous lemur groups contained several adult males and females and strong social relationships between specific males and females were evident based on nearest neighbor data. The goals of this study are: 1) to test the predictions outlined above, 2) to suggest that the term dyad or triad is more appropriate than "pair-bond" for the social organization of this species, and 3) to assess alternative explanations for the presence of male-female dyads within social groups.

MATERIAL AND METHODS

Study site

The study site was located in the Ranomafana National Park (RNP), between 47°18'–47°37' and 21°02'–21°05' in southeastern Madagascar. The Vatoharanana site is approximately 5 km south of the main research station, located near the village of Ranomafana. The Vatoharanana site consists of a high montane rainforest (1,125 m) with an annual rainfall of 2,300 mm during the 1988–89 study period. Predominant plant families in this region are Myrtaceae, Sapotaceae, Rubiaceae, and Lauraceae and phenological patterns are variable from year to year (Hemingway, 1995; Overdorff, 1996b). This region supports 11 other sympatric species of primates in addition to the rufous lemur.

Sampling methods

One primary group (Group I) of rufous lemurs (*Eulemur fulvus rufus*) was studied from July 1988 through August 1989, April through June, 1990, and from June through July 1995 with the help of a field assistant. A second rufous lemur group (Group II) was followed opportunistically throughout the first two study periods and was last seen at the study site in August 1993. It is presumed that Group II either migrated elsewhere or disbanded. Rufous lemur groups consist of multiple adult males and females (Table 1)

TABLE 1. Group composition of rufous lemur study groups during each of the three study periods

	# Adult males	# Adult females	# Juveniles
Group I:			
1988–1989	5	2	2
1990	5	4	0
1995	5	2	0
Group II:			
1988–1989	3	3	1
1990	4	3	2

and there is no evidence of female bonding, female dominance, or any dominance hierarchy (Vick and Conley, 1976; Vick and Pereira, 1989; Pereira et al., 1990; Pereira and Glynn, submitted).

Individual group members were captured using the Pneu-Dart™ system (Glander et al., 1991) and each adult individual was fitted with a unique nylon collar and metal tag for long-term identification. Each time an animal was captured they were weighed, measured, and age was estimated based on tooth wear. Blood also was drawn from most study subjects captured between 1988 and 1990 for DNA fingerprint analysis to assess relatedness and possible paternity (Merenlender, 1993).

Each observer followed an adult male and female focal animal on each sampling day during the first two study periods as part of a long-term study on the ecological correlates to social structure. Observers specifically focused on social organization during the 1995 study period. Focal animals were selected randomly and followed from 10–12 hours daily (approximately from dawn to dusk, depending on season). Each individual was followed for two hours at a time and samples were balanced across all adult group members.

Two methods were used to collect data during all-day samples: scan sampling and all occurrences of feeding, grooming, and aggression. Scan samples were collected on each focal animal at five-minute intervals to collect data on social behavior, activity, and habitat use. The following data were collected during each scan: focal animal's activity, nearest neighbor (defined as the individual(s) closest to the focal animal within 5m), substrate, and height (using 2m intervals). Activity, ranging, and habitat use patterns

are reported elsewhere (Overdorff, 1993a, 1996b).

All feeding bouts initiated by the focal animal were recorded to assess differences in individual food intake. The duration of each feeding bout and the type of food consumed were noted. Feeding bout length was determined by recording the time (hour, minute, and seconds) the focal animal started (placing food in the mouth) and stopped feeding on a food source. A bout was considered to have ended if the focal animal paused from feeding for 15 seconds or longer. Food type was categorized by the food item eaten by the focal animal and the plant species (Malagasy vernacular name or scientific name if known). Food items were categorized as ripe or unripe fruit, new or mature leaves, flower parts, or as miscellaneous material (see Overdorff, 1993b, for summary of dietary patterns). During the 1988–1989 study period, the number of food items consumed per bout was counted for each focal animal when possible. These data were used to calculate mean number of fruit consumed per minute of a feeding bout. Scan sampling was continued during all feeding bouts so that the focal animal's nearest neighbor could be determined.

Aggression within groups was recorded on an all-occurrence basis. In each case, the following information was collected: identity of individuals involved, context of aggression (feeding or nonfeeding), beginning and end time of bout (if greater than 15 seconds) and type of aggression (cuff, displacement, chase, push, lunge, squeal).

The only deviation from the sampling regime occurred during the mating season in 1989 (Group I: May 15–May 19) and 1990 (Group I May 2–May 9; Group II: May 12–May 17). Once females appeared to be sexually attractive to males (determined by increase in anogenital sniffing, licking, and attempted mounts), observers exclusively followed one adult female as their focal animal and the group was followed on consecutive days until preceptive and receptive behaviors were no longer observed (following Vick and Conley, 1976) to ensure that all observable diurnal copulations were recorded. All occurrence data on mating behavior was collected as follows: identity of male

and female involved in the mating interaction, who initiated a copulation (the female if she backed up against the male and had tail out of the way, or male if he approached the female, sat down, and sniffed or licked anogenital region and then mounted), number of mounts, and if ejaculate was observed.

Determining pair-bonds

Social organization was described within each social group using the scan sample data on nearest neighbor patterns. There are two major problems inherent in scan sampling: the fact that focal animals are sampled repeatedly and that data points are not necessarily independent. Therefore, a "runs-tests" (Sokal and Rolf, 1981) was conducted to determine independence of data points for nearest neighbor data. Independent data points were used for analysis.

Nearest neighbor scans were independent at half hour intervals and these data were used to create nearest neighbor association matrices as described in White and Burgman (1990):

$$(x_{ij} + x_{ji}) / (n_i + n_j)$$

where x_{ij} was the number of scan samples in which i is j 's nearest neighbor, x_{ji} was the number of scans in which j is i 's nearest neighbor, and n is the total number of scans collected on i and j .

Cluster analyses were performed on nearest neighbor association matrices using the NTSYS computational package (UPGMA; Rohlf, 1985) to obtain two-dimensional graphic representations (dendrograms) of the relationships between individuals within social groups. Matrices were constructed using nearest neighbor data collected from August 1988 through August 1989 from each study group to examine feeding, non-feeding, and grooming contexts within the following four reproductive periods: 1) Gestation (assumed after last day of copulation until birth of infant), 2) Lactation I (first three months after birth), 3) Lactation II (fourth to sixth months after birth), and 4) Mating season (dates above). Nearest neighbor relationships also were examined for May–July 1988 when fruit was least available (Overdorff, 1996a). The scan samples collected in 1990 and 1995 were

used to generate two dendrograms for feeding, nonfeeding, and grooming contexts within each study period. The 1990 field season corresponded to the mating season and the first two weeks of gestation and the 1995 field season corresponded to gestation.

Two statistical tests were conducted using the nearest neighbor association matrices. First, how well a dendrogram represented an association matrix was determined using the cophenetic correlation coefficient (r). Correlation coefficients greater than 0.80 indicated that dendrograms accurately portrayed data within an association matrix (Sokal and Rohlf, 1962). Dyads or triads were determined using these graphic representations.

Second, association matrices were compared to one another using a Mantel test (Mantel, 1967; Schnell et al., 1985) and cophenetic correlation coefficient (r). Two thousand random permutations were performed on the rows and columns of comparison matrices; the Mantel t statistic and correlation coefficient was considered significant at $P < .01$ level (meaning that matrices were significantly correlated, $r \geq .80$). In this analysis, the maximum number of permutations resulting in an r value less than 0.80 for correlations where $r = .80$ or greater was 7 (out of 2,000). Further details on the methods used for nearest neighbor relationships can be found in White and Burgman (1990).

Aggression

Rates of aggression were examined by context and reproductive periods and G tests were used to determine if aggression rates varied by sex of interactor (male–male, male–female, or female–female interactions) or partners (partners were identified using dendrograms generated from the nearest neighbor data). Comparisons were made within study periods between feeding and nonfeeding contexts and by reproductive periods when more than one period was sampled.

Food intake

The amount of food consumed per minute (feeding rate) for each feeding bout were compared using a Kruskal Wallis test for when an individual fed alone, with a male

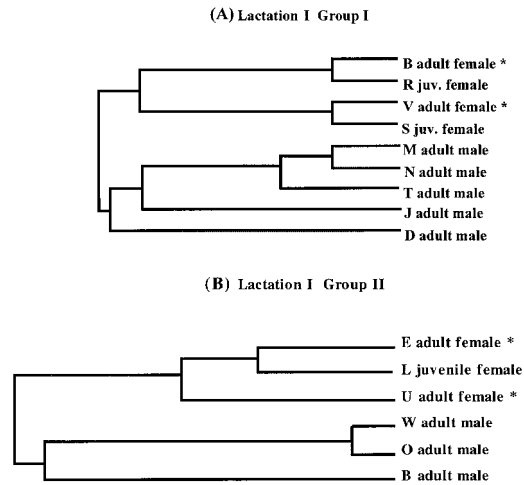


Fig. 1. Nearest neighbor relationships during the first three months of lactation (September–November, 1988) for Groups I and II (matrix fit A: $r = .90$ B: $r = .85$); * indicates females who gave birth to an infant at this time.

dyad partner, or with another group member (nondyad partner, male or female). Individual feeding rates also were compared to determine if members of a dyad ate more or less fruit per minute when feeding near each other. Fruit comprised the majority of their diet and only feeding rates on fruit were used. Food items were grouped by size of food item (small, medium, and large) following Overdorff (1996a) so that only feeding rates on similar-sized food items were compared. This analysis was conducted using only data collected from the first study period.

RESULTS

Predictions 1 and 2

Consistent, distinct dyads between adult males and females were not observed, although subgroups consisted of 1) a male, female, and juvenile female, 2) adult female and juvenile female, or 3) two or three males (Figs. 1, 2). Subgroup membership also varied throughout the year and by study period (Table 2). During Lactation I, females tended to isolate themselves from other group members except their yearling offspring (Fig. 1) rather than form dyads with males.

In contrast, distinct dyads of adult males and females were observed during the 1989

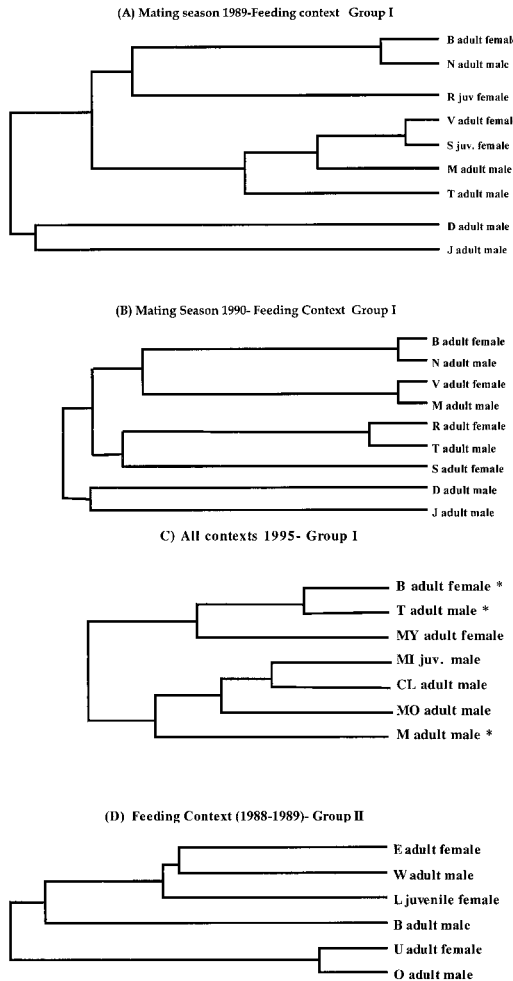


Fig. 2. Dendrograms representing nearest neighbor relationships for rufus lemur Group I from August 1988 through August 1989. (A) Dendrogram showing nearest neighbor patterns while feeding during the 1989 mating season (matrix fit $r = .97$). Nearest neighbor patterns while group members were feeding during May, June, and July were similar (matrix correlation $r = .92$). See Table 2 for correlation values. (B) Dendrogram showing nearest neighbor patterns while animals were feeding during May 1990 (matrix fit $r = .94$). (C) Nearest neighbor dendrogram for 1995 field season (matrix fit $r = .92$); * indicates original group members. 1 = MY is presumed to be B's daughter, born in 1991. (D) Nearest neighbor dendrogram for Group II (for all periods during Study period 1) while individuals are feeding (matrix fit $r = .87$). See Table 2 for matrix correlations between periods.

and 1990 mating seasons, specifically while feeding (Fig. 2, Table 2). The same pattern was observed while animals fed during May–July 1989, which correspond to the first two

months of gestation (May 1989 vs. May–July 1989: $r = .95$, $t = 5.94$, $P < .0001$) and was a period of extreme food scarcity (Overdorff, 1996a).

Prediction 3

Females did not exclusively copulate with a particular male in the study group and mated with all males during their cycle. However, there was a trend during both mating seasons for females to copulate first during the first two days of their cycle with males who acted as dyad partners while feeding. Peripheral males and males who did not act as dyad partners tended to mate later in the females cycle (Fig. 3).

Prediction 4

Male dyad partners vs. nondyad partners. Higher rates of aggression were observed between males and nondyad members but were context-specific. Rates of aggression were higher between males and females in feeding than nonfeeding contexts during Lactation I and the 1989 mating season (Lac I $G = 8.41$, $df = 2$, $P < .01$; Mate89 $G = 123.32$, $df = 2$, $P < .0001$). Specifically, males initiated more intra-sexual bouts of aggression than expected towards juvenile females (52%, $n = 24$) or females who were not their partner (33%, $n = 15$). The remaining bouts were initiated by the female towards their male partner (15%, $n = 7$). Aggression was not observed during feeding in the 1990 field season and only 13 bouts of aggression were recorded during the 1995 study period between T and MY (B's adult daughter); all occurred while feeding.

Male-male aggression. Patterns of aggression between males varied between the two mating seasons. Male-male rates of aggression were not higher than expected during the 1989 mating season. In contrast, male-male aggression was significantly higher during the 1990 mating season ($G = 33.83$, $P < .0001$, $df = 2$, Fig. 4c). Males who functioned as dyad partners (N, V, M) chased peripheral males (D, J) from receptive females at this time. Only 12 bouts of aggression were recorded in Group II but patterns

TABLE 2. Statistical results from Mantel tests comparing nearest neighbor patterns by context within and between reproductive time period (first three months of lactation, last three months of lactation, mating, and gestation) in Group I and Group II

Context compared within reproductive period:		Group I		Group II	
		r ¹	t ²	r ¹	t ²
Lactation I (88–89)	Feeding vs. nonfeed	0.92	5.44	0.98	5.96
Lactation II (88–89)	Feeding vs. nonfeed	0.93	5.53	0.82	4.72
Gestation (88–89)	Feeding vs. nonfeed	0.81	4.68	ND ³	ND
Mating 1989	Feeding vs. nonfeed	0.68⁴	3.96	ND	ND
Mating 1990	Feeding vs. nonfeed	0.23	1.39	0.93	5.54
Gestation 1995	Feeding vs. nonfeed	0.84	3.93	ND	ND
Reproductive periods compared (1988–89)					
Lactation I	Lactation II	0.42	2.43	.32	1.90
Lactation I	Mating-feeding	0.08	0.48	.07	0.46
Lactation I	Mating-nonfeed	0.54	3.25	.25	1.10
Lactation I	Gestation	0.54	2.65	ND	ND
Lactation II	Gestation	0.85	5.07	ND	ND
Lactation II	Mating-feeding	0.56	3.13	.84	5.12
Lactation II	Mating-nonfeed	0.78	4.45	.81	4.91
Gestation	Mating-feeding	0.43	2.80	ND	ND
Gestation	Mating-nonfeed	0.86	5.10	ND	ND

¹ r = correlation coefficient.

² t = Mantel t score.

³ ND = no data available or sample sizes were too small.

⁴ Bolding indicates matrices that were not correlated with one another.

Significance level was set at $P < .01$, $r > .80$.

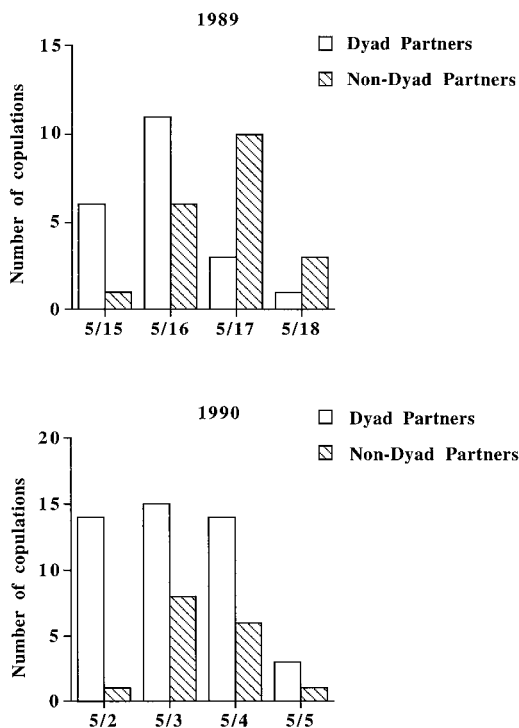


Fig. 3. Order and number of copulations for each female that was receptive from May 15–May 18, 1989, and May 2–May 5, 1990, in Group I. Each graph represents each male's successful copulations (ejaculate observed) for females B and V (1989) and B, V, R, and S (1990).

were similar to those observed in Group I: all bouts occurred between adult male W and peripheral male B when B approached any of the cycling females.

Males did not aggress against each other more often during the birth season, as predicted. Direct observations of males trying to attack infants were also not observed, although one incident that I observed has been incorrectly cited as an infanticide. The day after V in Group I gave birth in September 1988, N and M (who was her preferred partner) consistently followed and displaced her and her yearling offspring. They were never observed to aggress towards either individual, grab the infant, or actively chase either V or S. One and a half weeks later, V's infant disappeared. No body was found nor was either male observed to kill the infant. It is also important to note that all infant disappearances observed during this study ($n = 11$) did not coincide with the addition of new group members.

Male–female aggression. Rates of aggression were higher than expected between males and females during the first half of lactation, as predicted, as well as the 1989 mating season (Lac I G = 6.70, $P < .04$, $df = 2$; Mate89 G = 27.58, $P < .0001$, $df = 2$; Fig. 4 A,B).

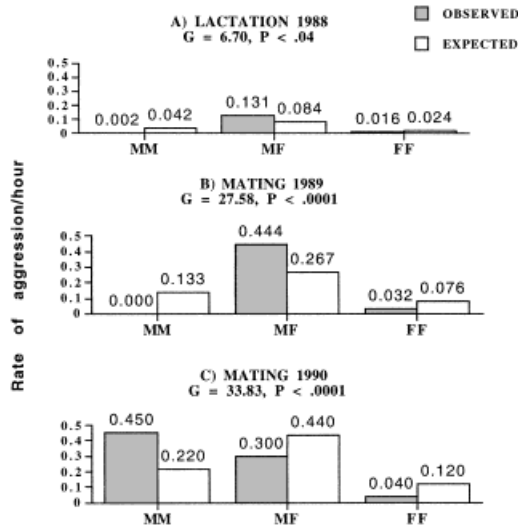


Fig. 4. Observed and expected rates of aggression for rufous lemur Group I for A) Lactation I (mid-September–mid-December 1988), B) mating season 1989 (May), and C) mating season 1990 (May).

Influence of dyads on food intake

Individual fruit intake varied depending on who was the focal animal's nearest neighbor. Feeding rates did not differ for small ($H = 0.62$, $df = 5$, n.s.) or large fruits ($H = 6.12$, $df = 4$, n.s.) but the identity of the nearest neighbor affected feeding rates on medium-sized fruits (Fig. 5, $H = 11.65$, $df = 4$, $P < .02$). Most adult females (E, B, U) had equal or higher feeding rates when feeding with an adult male partner than with other individuals (Fig. 6). Rates, however, were highest when feeding alone.

DISCUSSION

Infanticide prevention hypothesis

Males do not appear to remain near females for the purpose of infanticide protection based on results from this study. Adult males were not in close proximity to their female dyad partner during the most critical times (i.e., mating and birth seasons), aggression was not consistently observed between males or directed towards males by females during the birth season, and females did not copulate exclusively with one male. In general, rufous lemurs formed smaller subgroups of two or three individuals within the

larger social group but these subgroups were not exclusively comprised of one male and female. Male–male and female–female dyads also were observed consistently. In addition, one or two males were peripheral to the remaining group members (referred to as the social core) in each social group during each study period.

Nearest neighbor relationships also were not stable year-round and varied with context, reproductive period, or the study year. The individuals who formed male–male and female–female dyads were generally consistent within study periods but adult male–female dyads were more context-dependent. Specific males and females maintained spatial proximity more often in Group I while feeding during the most severe period of food scarcity (May, June, and July 1989) and May and June 1990 when an unusual peak in food availability occurred (also the mating season). Male–female dyads formed during feeding year-round in Group II. The significance of these patterns is discussed below in the section Alternative explanations for male–female relationships.

Nearest neighbor patterns also shifted with a change in a female's reproductive status, but only during early lactation. Females with new infants were more spatially isolated from other group members and males spent more time in proximity to one another. If a male's specific role is to protect vulnerable infants, then males should have maintained closer proximity to their specific female partner and her infant when the

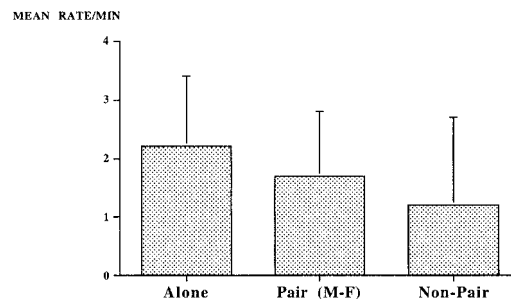


Fig. 5. Mean feeding rate per minute on medium-sized fruit when rufous lemurs were alone (no nearest neighbor within 5m), with a preferred partner (as determined by dendrograms), or with a nonpartner as a nearest neighbor.

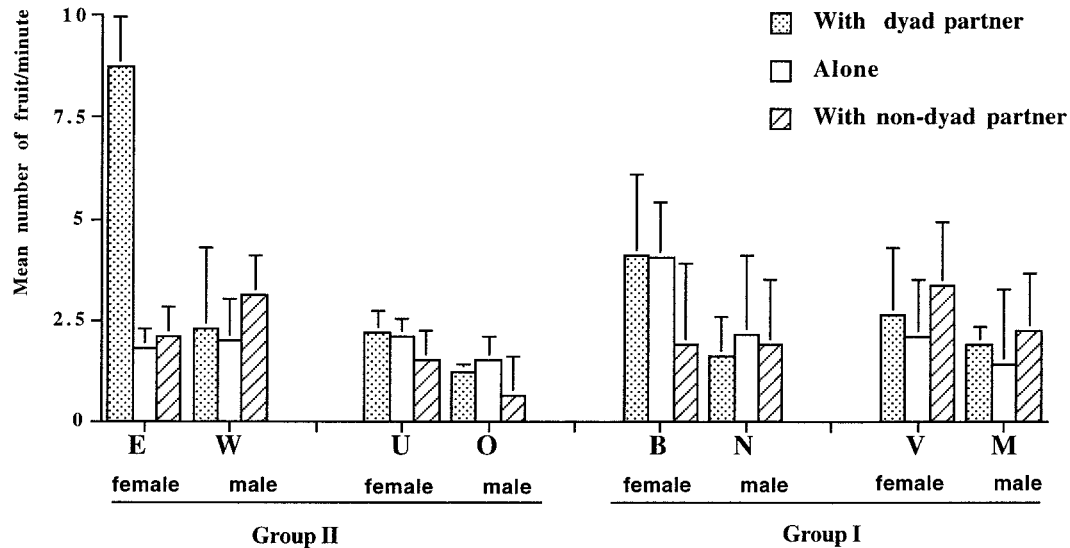


Fig. 6. Mean feeding rate on medium fruits by partners. E-W and U-O are from Group II and B-N and V-M are from Group I. Data from 1988–1989 field season.

infant would be most vulnerable to attack. Although these patterns do not support the original prediction, it could be argued that the observed spatial relationships could be a female counterstrategy to protect her infant by physically isolating herself and her infant from potentially infanticidal males. It has been suggested that female lions adopt a similar strategy when lion cubs are most vulnerable to infanticide attacks (Grinnell and McComb, 1996).

This alternative explanation is problematic for two reasons. First, the cause of infant deaths is inconclusive. Contrary to what has been previously reported (van Schaik and Dunbar, 1990), infanticide or infanticidal attempts have never been observed in this species in the wild. Infant disappearances also did not correlate with the addition of a new male into the group, so that infanticide cannot be inferred. In addition, infanticides have been not observed in western populations of rufous lemurs or other *E. fulvus* subspecies (Sussman, personal comm.; Freed, personal comm.).

The second problem is that potentially infanticidal males could risk killing their own infant, because they could not be certain of paternity based on the observed copulation patterns. Some males copulated

more often and earlier during a female's cycle than other males, but adult males did not form consortships with reproductive females. Males that were members of the social core of the group (e.g., Group I: N, M, T, or Group II: W, O) copulated slightly more often than peripheral males (D, J, or B), and were the same males that females were likely to feed near a female. During the first mating season, adult male N (Group I) copulated almost twice as often than other males, although he was unable to monopolize copulations with a single female. Vick and Conley (1976) and Pereira and McGlynn (submitted) reported a similar pattern in captive populations of *E. fulvus* although, during their studies, one male was able to exclusively copulate with individual females.

The less than predictable nature of the food supply and the number and timing of cycling females in a group may play a role in the differences observed between the mating behavior in wild and captive populations. These variables also may explain the differences observed in rates of aggression, number of copulations, and copulation order between Group I's mating seasons. The most extreme changes in fruit availability were observed before, during, and after the mating season in 1989 and 1990. Fruit was most

scarce from May–July 1989 but the highest peak in fruit availability was observed the following year during May and June 1990 (see Overdorff, 1996a). The number of reproductive females in Group I also doubled during the 1990 mating season when S and R cycled for the first time.

During the 1989 mating season, when fruit was most scarce and only two Group I females cycled, aggression rates between males were lower than expected and most of the aggression observed occurred between male and female nonpartners while feeding. Fewer copulations were observed and rufous lemurs spent more time feeding than resting or traveling (Overdorff, 1996b). The extreme scarcity of food may have constrained the amount of energy available for aggression and controlling access to reproductive females. Because only two females cycled, individual males may have had a better opportunity to monopolize copulations and monitor changes in the female's reproductive state.

During the 1990 mating season, when food was more available and four females cycled within a five-day period in Group I, aggression occurred primarily between males in nonfeeding contexts (N or M chasing peripheral males D and J away from cycling females), more copulations were observed than in the previous year, and the animals rested more instead of feeding (Overdorff, unpublished data). A male's ability to monopolize copulations or copulate more frequently appears to decrease with the number of cycling females. Increased food availability may allow for more time and energy to be devoted to monitoring receptive females and mating activity in general. Aggression also typically increases among anthropoid males, with a corresponding increase in cycling females (Smuts, 1987).

Because this species is cathemeral (Overdorff and Rasmussen, 1995), consistent observations during nocturnal periods are necessary to confirm if the diurnal copulation pattern is consistent, since van Schaik and Kappeler (1993) speculated that adult males may be able to more effectively monopolize a specific female at night.

Alternative explanations for male–female relationships

Infant care. Many researchers have noted the strong social ties between males and their infants in monogamous primates where males care for infants intensively (Wright, 1990) or in larger social groups where males provide more indirect forms of male care. Although rufous lemur males do not carry or share food with infants, they may provide less direct forms of infant care by protecting infants from aggression by other group members or allowing infants to feed near them when infants begin to locomote independently. Unfortunately, this prediction is difficult to test because the infants born during the longest study period died at one month and three months of age in Group I. In Group II, both infants survived but this group was not observed as consistently as Group I.

Based on what observations could be made, rufous lemur males were interested in newborn infants (e.g., N and M showed interest in V's infant in 1988) but females separated themselves from males during the first four weeks after birth. As described above, it is unlikely that females are avoiding infanticidal males; instead, they may be minimizing energy costs since they are relatively inactive compared to males at this time (Overdorff, unpublished data). They may also minimize the degree of possible competition from other group members for resources such as sleep sites or food. Sauther (1992), for example, found that female *Lemur catta* do not tolerate males as nearest neighbors during critical times of the year. These may be some of the additional ways that females try to minimize energy costs when reproductive (see Tilden and Oftedal, 1995). Finally, males appear relatively uninterested in juveniles. Juvenile females slept and fed near their mothers rather than adult males and the majority of the bouts of aggression occurred between male and juvenile females in Group I. Based on these observations, it does not appear that males provide any concrete services for infants or juveniles.

Vigilance and predation. Vigilance and predator detection are other services that

males could provide for females and infants. Males, therefore, should be more responsible for scanning and detecting predators than females. Gould (1996b) also suggested that strong affiliative relationships between male and female *L. catta* may benefit males by providing increased safety from predators because they are able to remain within the social core of a group. This same benefit may apply to rufous lemur males as well. Vigilance behavior by rufous lemurs has not been as rigorously quantified as in other lemur species such as *L. catta* (Gould, 1996), although scanning the environment was recorded as an activity during the 1988–89 field season and may be some measure of vigilance behavior. This activity was not recorded often (189 scan samples during the entire study period) and females were primarily responsible for monitoring the environment (89%), not males. Females also were responsible for making the initial alarm call on six occasions when large birds were detected near the social group. Males that formed dyads with females, however, were also members of the social core and may gain increased predator protection over peripheral males, particularly if females are quicker to detect a predator's presence. Although males do not actively monitor their environment, they may function as low-cost sentinels, as described by Sauther (1993).

Thermoregulation. Morland (1993) pointed out that huddling behavior among lemurs may be one way of conserving energy during cold weather since prosimians are not as efficient at thermoregulation compared to other primates. Smaller subgroups of rufous lemurs may form to stay warm since minimum temperatures can reach 30°C during certain seasons. This particular hypothesis may also account for the variation observed in subgroup membership. A rufous lemur female does not necessarily have to huddle with a male, but could pair with a member of the same sex. Based on this hypothesis, one could predict that subgroups should not be as distinct during warmer seasons and that individuals who are not consistently members of dyads or trios are less likely to survive. However, rufous lemurs appear to maintain distinct subgroups throughout the

warmer months, when temperatures are as high as 30°C. In Group II, one peripheral individual (male B) rarely paired with other members and remained in his group until the group disappeared in 1993.

Protection from general aggression. A variation of the infanticide prevention hypothesis is that males and females affiliate so that males can provide females protection from general aggression from other group members, not specifically infanticidal males (Smuts, 1985; Rose, 1994; Manson, 1994). Unlike anthropoids, lemurs are monomorphic (Glander et al., 1991) so that there is no particular size advantage to a female by having a male as a partner. A male, however, is not under the same energetic constraints as a female, particularly when she is reproducing. Thus he may be a more reliable choice as a "protector" than another female. Nevertheless, male–female dyads were most prominent during feeding, which implies that it may be most beneficial for males and females to form partnerships only during specific times of the year in specific contexts to mediate aggression.

Male and female reproductive strategies and food intake. Based on the data presented above, males and females may form dyads in certain situations. Most adult male and female dyads had higher feeding rates when feeding near each other, and most females appeared to benefit by having higher feeding rates with dyad partners than when feeding near other individuals. Similar results have been observed between males and females during experimental manipulation of food in captive *E. fulvus* populations (Anderson et al., 1992).

Feeding rates, however, were highest when individuals fed alone, so why do rufous lemurs tolerate any nearest neighbors when feeding, as seen in *L. catta* females (Sauther, 1992)? Rufous lemur dyads during feeding may be linked to their unclear dominance hierarchy, the distribution and density of food patches, and vulnerability to predators. Unlike *L. catta*, rufous lemurs are not clearly female dominant (Pereira et al., 1990) and dyads between individuals may help miti-

gate within-group competition when feeding, particularly if food is scarce. If a female needs assistance defending a feeding site, her most recent offspring would not be the best choice as a partner because they have not yet reached adult body size. Another female would be subject to the same reproductive and energetic constraints (particularly during gestation) and may compete for access to the best quality food (Wrangham, 1980). Therefore, males may be the best choice under these circumstances.

Individuals fed alone most often when patches were large and clumped (see Overdorff, 1996a), so that group members were within visual and vocal contact but did not necessarily have a nearest neighbor within five meters. Having a nearest neighbor while feeding when patches are smaller and more widely distributed may increase predator detection, although the evidence summarized above for this assumption was weak. By feeding alone, individuals may be more susceptible to predators.

A more robust test of this hypothesis would be to determine if females who have male dyad partners also benefit in terms of long-term reproductive success. For example, male *Cebus apella* have higher mating success with females when they defend individual food sources for females (Janson, 1986). Data are limited due to the high infant mortality rate, although there is weak evidence that females who consistently used male partners while feeding also reproduced successfully (Overdorff, submitted). In Group II, for example, females with male partners reproduced successfully each year. The reproductive pattern in Group I, however, was a bit more complex. Female B consistently had a male nearest neighbor while feeding and produced more offspring than other females. Younger female R also reproduced successfully in 1990 and was observed to have a male partner when feeding earlier in the year. Female V did not reproduce successfully in 1988; she fed most often near her daughter S and less often near two males (M and T). In 1990, M was consistently her nearest neighbor while feeding and she reproduced the following birth season. Unfortunately, nearest neighbor data was not collected in the time periods between study

periods so it is impossible to know if changes in nearest neighbor relationships could have affected infant survival rates for other years.

Males may receive both feeding and long-term reproductive benefits by pairing with females. Males who paired with females while feeding usually had first access to large fruit patches by entering at the same time as females (Overdorff and Erhart, in preparation) while peripheral males and juveniles waited for them to finish feeding. Males may also obtain higher quality food by feeding near a female, although this hypothesis needs to be directly tested. Within the pair, male feeding rates were lower, although their feeding rates were higher than when they fed near other group members. One of the possible reasons male feeding rates were lower is that they interrupted their feeding bouts more often to chase or displace other group members who approached the pair while feeding, particularly when food was scarce.

Males may have some long-term reproductive success by assisting females while feeding, although not as a full-time consort. Male partners copulated first and slightly more often than peripheral males, and females may perceive males who assist during feeding as good mate choices. For example, four out of five infants were fathered by males who acted as dyad partners (Merenlender, 1993). A larger sample size of known paternity and consistent observations across mating seasons can help discern the reproductive impact of a consistent dyadic relationship between males and females.

In conclusion, the infanticide prevention hypothesis does not seem to offer the best explanation for why rufous lemurs form social relationships between specific adult males and females. Dyads of males and females formed often in feeding contexts and females appeared to rely on males as a means of resource defense, which could ultimately influence the reproductive success of females. Males may benefit by greater food intake or access to higher quality food. Males also may benefit if their partnerships confer reproductive advantages by being able to mate first or slightly more often than other males. Although there was weak support for other possible benefits such as predator

detection and thermoregulation, further study may reveal that males and females may receive multiple benefits from strong social relationships with each other.

Does the term pair-bonding necessarily apply to this population of rufous lemurs? If the original definition of "a close social relationship between two individuals" is used, then pair-bonding is applicable. The underlying implication, however, is that pair-bonding occurs consistently and solely between adult males and females despite the fact that the sex of the individuals is not explicitly included in the definition. A term such as "friendship" (Smuts, 1985), or a more simple and descriptive term such as "dyad" or "male-female affiliative relationship" would be more appropriate because: 1) the exact reproductive benefits of male-female dyads are unclear, 2) same-sex dyads were observed, and 3) nearest neighbor relationships changed based on context, reproductive state, and study period.

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